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Current climate, but also long-term climate changes and human impacts, determine the geographic distribution of European mammal diversity

Running title: Determinants of European mammal diversity

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Biosketch: Ana M. C. Santos is interested in community ecology, island biogeography and macroecology. Her current work focuses on cross-scale variations of community assembly and structure, and on the impacts of global change on ecosystem functioning. All co-authors work in macroecology and biogeography.

Abstract:

Aim. Historical climate variations, current climate and human impacts are known to influence current species richness, but their effects on phylogenetic and trait diversity have been seldom studied. We investigated the relationship of these three factors with the independent variations of species, phylogenetic and trait diversity of European mammals. Considering the position of the 0ºC isotherm in the Last Glacial Maximum as a tipping point, we tested the following hypotheses: northern European assemblages host less species than southern European ones; northern areas harbour trait and phylogenetically clustered assemblages, while the more stable southern areas host random or overdispersed assemblages; and, species richness increases with human influence, while phylogenetic and trait diversity show clustered patterns in areas with stronger human influence.

Location. Western Palearctic.

Time period. Current and Late-Pleistocene effects on present-day diversity.

Major taxa studied. Terrestrial mammals.

Methods. We used a novel analytical approach based on distance matrices to separate the independent variations of species, phylogenetic and trait diversity, and assessed their relationships with current climate, climate stability and human influence through structural equation models.

Results. The species-poor assemblages from northern Europe show higher phylogenetic and trait clustering than the more stable richer southern areas. However, no assemblage presented trait nor phylogenetic overdispersion. Current climate is the primary driver of phylogenetic and trait diversity, while species richness is affected similarly by both current and past climates. Higher

human influence correlates positively with species richness and trait diversity, both directly and by mediating indirect effects of present climate.

Main conclusions. Current climate, climate stability and human influence affect the studied aspects of diversity, although the form and magnitude of their effects varies through space. Importantly, higher levels of human disturbances correlate with more speciose and trait diverse assemblages, an apparently counterintuitive result that deserves further study.

Keywords: Community structure, functional traits, glaciations, global change, human impact, phylogenetic diversity, species richness, structural equation models, trait diversity.

1. Introduction

Geographic patterns of biodiversity result from evolutionary and ecological processes determining the increase, maintenance and depletion of species, lineages and ecological traits through time (Wiens & Donoghue, 2004). Species distributions are affected by different abiotic factors, including climatic conditions and historical events, biotic interactions and human impacts (e.g. Faurby & Svenning, 2015; Hortal, Lobo, & Jiménez-Valverde, 2012). Understanding the importance of each one of these factors on the distribution of biodiversity is fundamental for managing the current biodiversity crisis (Kerr, Kharouba, & Currie, 2007). However, most research efforts have focused on species richness, with much still to be explored in what concerns other facets of biodiversity, such as phylogenetic or trait diversity. These two aspects of biodiversity may reflect the potential of species to maintain ecosystem functioning and acquire novel evolutionary pathways for coping with environmental changes (Díaz et al., 2013; Violle, Reich, Pacala, Enquist, & Kattge, 2014; Schipper et al., 2016).

Current climate is strongly associated with species richness, mainly through energy and water budgets (e.g. Currie, 1991; Whittaker, Nogués-Bravo, & Araújo, 2007), and also with trait (i.e., functional) and phylogenetic diversity (e.g. Barreto, Graham, & Rangel, 2019; Safi et al., 2011). These factors are important drivers of the geographic distribution of different groups of organisms, either acting through primary productivity (e.g. Araújo et al., 2008; Barreto et al., 2019; Fløjgaard, Normand, Skov, & Svenning, 2011; Safi et al., 2011), filtering on species climatic tolerances –particularly at higher altitudes and latitudes (Hawkins et al., 2003; Hortal et al., 2011), or affecting mutation and speciation rates (Wiens & Donoghue, 2004). Pleistocene climatic oscillations also left a strong imprint on the current distribution of many species (Sandel et al., 2011) – particularly in high latitudes (Dynesius & Jansson, 2000), as well as on extinction rates

(Nogués-Bravo, Ohlemüller, Batra, & Araújo, 2010) and community structure (Rowan, Kamilar, Beaudrot, & Reed 2016; see also Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015). These effects are particularly evident in Europe (Araújo et al., 2008; Calatayud et al., 2016, 2019; Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013; Hortal et al., 2011; Ordonez & Svenning, 2016; Svenning & Skov, 2004; Svenning et al., 2015), where many species went extinct in the glaciated northern latitudes during the ice ages. However, species holding certain traits and belonging to particular clades were either able to persist in those areas (for example, by regulating body temperature), or to survive in southern, more climatically stable refugia (e.g. Rodríguez, 2006). Many of these species recolonised northern Europe after the glaciers retreated (Hewitt, 1999), resulting in varying distribution patterns that are thought to be mainly associated with their dispersal capacity, ability to occupy multiple and fragmented habitats and/or physiological tolerance limits (Hortal et al., 2011; Ordonez & Svenning, 2015; Svenning & Skov, 2004). Therefore, biotas from areas that underwent profound Pleistocene climate changes tend to show clustered phylogenetic and trait structure, i.e. communities from these areas include species that tend to be more similar in terms of phylogenetic relationships and traits than expected by chance (e.g. Calatayud et al., 2019; Ordonez & Svenning, 2015; Pinkert et al., 2018). As a consequence, the 0°C isotherm at the Last Glacial Maximum (LGM, around 21,000 yr bp) is still the northern limit of the distribution of different taxonomic groups in Europe today (e.g. Araújo et al., 2008; Hortal et al., 2011). Indeed, the past location of this isotherm roughly coincides with the shift in the sign of the species–energy relationship for mammals (Whittaker et al., 2007).

Human activities also affect biodiversity, altering the functioning of ecosystems (Pimm et al., 2014) and promoting changes in the Earth's climate and environmental conditions (Zalasiewicz et al., 2008). Importantly, they have changed current diversity patterns (Faurby & Svenning, 2015),

highlighting the importance of including human-related effects on large-scale studies focusing on diversity drivers. These human impacts are not restricted to post-industrial times (Polaina, González-Suárez, & Revilla, 2019). Instead, humans have long been an important driver of species range contractions and extinctions (Sandom, Faurby, Sandel & Svenning, 2014). The interaction between increasing human pressure and climate changes during the Late Quaternary led to the extinction of many Holarctic large mammals from particular lineages and with specific traits (e.g. Davis, Faurby & Svenning, 2018; Lorenzen et al., 2011; Nogués-Bravo, Rodríguez, Hortal, Batra, & Araújo, 2008; Wan et al. 2019). Indeed, some mammal traits reflect the species' susceptibility to anthropogenic pressures (Fritz et al., 2009; Wan et al. 2019), so that the current patterns of trait and phylogenetic diversity may have been shaped by non-random human-driven extinctions (Faurby & Svenning, 2015). Paradoxically, human presence is positively correlated with mammal species richness in many regions, including Europe (Araújo, 2003; Luck, 2007; Torres-Romero & Olalla-Tarraga, 2015; but see Barbosa, Pautasso & Figueiredo, 2013). Both humans and other mammals have for long held larger and more diverse populations in areas that currently show higher productivity or certain climates (Balmford et al., 2001; Fjeldså & Burgess, 2008), or that had higher climate stability during the Pleistocene (Fjeldså & Rahbek, 1998, cf. Araújo, 2003).

The relationships between species richness and current climate, climate change and anthropogenic effects are relatively well known (e.g. Svenning et al., 2015), whereas the effects of these factors on the geographical patterns of phylogenetic and trait (i.e., functional) diversity have been less studied, particularly at large spatial scales (but see, e.g., Faurby & Svenning, 2015; Holt et al., 2018; Safi et al., 2011). Here we evaluate the large-scale patterns of species, trait and phylogenetic diversity of native European mammals, assessing the potential effects of current

159 climate, climate changes since the LGM, and human impacts. We do this through a novel statistical
160 approach that allows disentangling the independent effects of each facet of biodiversity.

161 Europe underwent significant climatic changes during the Pleistocene, of increasing
162 intensity towards the north. Therefore, we expect that both the distribution of biodiversity and the
163 relative importance of its drivers will differ between northern and southern European biotas (as
164 delimited by the location of the LGM 0° isotherm, see above). We predict that northern areas have
165 fewer species than the more climatically-stable areas of the south (H1). Also, northern areas will
166 harbour phylogenetically clustered assemblages, due to the importance of phylogenetically
167 conserved adaptations to cold environments or related with dispersal ability (H2.1). In contrast,
168 southern assemblages were less influenced by such filters, having experienced more climatically
169 stable environments that provided longer time periods for the evolution of communities
170 (Rodríguez, 2006); therefore, in general, southern assemblages should not be phylogenetically
171 clustered, exhibiting either no particular evolutionary pattern, or even phylogenetic overdispersion
172 (i.e. include species that are less related to each other than expected by chance) (H2.2). These
173 hypotheses also apply to trait diversity: northern biotas will tend towards trait redundancy (due to
174 the selection of traits related to the ability to colonise or persist in these areas) (H3.1), whereas
175 such clustering will not occur in southern assemblages. In this latter region, we expect a random
176 trait structure, or even trait overdispersion in those areas where long-term species interactions have
177 promoted limiting similarity processes (e.g. long-term competition reduced trait overlap) (H3.2).
178 We also expect that the diversity of northern assemblages is driven mainly by past climatic
179 conditions, while in the south it is primarily driven by current climate (predictions associated with
180 H1, H2.1, H2.2, H3.1 and H3.2). Regarding human impacts, we expect that species richness will
181 be higher in areas with stronger human influence (H4.1; see above); such areas will also present

phylogenetic and functional homogenization, which translates into phylogenetic and trait clustering (H4.2 and H4.3, respectively). Given the complexity of interactions between diversity, current climate, climate stability, and human impacts, we evaluate the concurring effects of all these factors using Structural Equation Models.

2. Methods

2.1. Data

Data on the distribution of native terrestrial (both volant and non-volant) mammal species were obtained from IUCN (2016). We used range maps instead of Atlas data, as the latter may include incomplete and uneven information on species distribution (see Hortal, 2008). We used a 100 km equal-area grid in order to minimize omission and commission errors, thus balancing data quality and resolution (Hortal, 2008; Hortal et al., 2011; Hurlbert & Jetz, 2007). So, range maps were reprocessed to obtain the occurrence of each species in a 100 km equal-area grid (i.e. with 10,000 km^2 cells) encompassing the whole Western Palearctic, i.e. both Europe and the Mediterranean region (European grid, based on the ETRS89 Lambert Azimuthal Equal-Area projection; it also includes the Mediterranean Islands and Northern Africa). This region hosts 357 mammal species, which constitute the regional pool of species that can potentially colonise any grid cell, and therefore were used as the source pool for all community assembly analyses described below. The extent of our analyses was limited to mainland Europe (comprising Great Britain and Russia up to the Ural Mountains), the Anatolian Peninsula, Syria and Israel. In total, these territories host 354 mammal species. We excluded cells that had less than 95% of land surface. Species richness was calculated as the number of species recorded in each grid cell.

Trait data were obtained from PanTheria database (Jones et al., 2009) and updated using additional sources (as in Hidasi-Neto, Loyola, & Cianciaruso, 2015; Safi et al., 2011). The selected traits relate to the type and quantity of resources used, and how and where these resources are acquired (Safi et al., 2011). These include: (i) body mass (in grams), (ii) diet (i.e. vertebrates, invertebrates, foliage, stems and bark, grass, fruits, seeds, flowers, nectar and pollen, roots and tuber); (iii) habitat (aquatic, fossorial, ground-dwelling, aboveground dwelling, aerial) and activity period (cathemeral, crepuscular, diurnal, nocturnal). When trait data were missing for a given species, median values for the genus were used. This occurred for 9.8% of the species, mainly in Rodentia, and for less than 5% of the cells of the trait by species matrix; after this process, only 0.4% of the cells of this matrix had missing data (mostly in activity period). We used a dated mammalian 'supertree' (Bininda-Emonds et al., 2007, updated by Fritz, Bininda-Emonds, & Purvis, 2009), modifying it according to the IUCN Red List taxonomic nomenclature (IUCN, 2016). Although some parts of the mammal phylogeny are still under discussion (e.g. O'Leary et al., 2013), this phylogeny remains as the most complete and stable for the whole Class (Daru et al., 2019), and is widely used in macroecological studies (e.g. Saladin et al., 2019).

Current and historical climate data were gathered from the ECHAM3 paleoclimatic model (Braconnot et al., 2007; processed as in Calatayud et al., 2016; Hortal et al., 2011), and included current temperature and precipitation, and temperature and precipitation stability since the LGM. These two latter variables correspond to the differences between current and LGM values, so smaller values indicate higher climate stability (Araújo et al., 2008; Hortal et al., 2011). Comparability between these variables was attained by extracting all information from the same Atmosphere-Ocean General circulation model, i.e. using a downscaled version of the ECHAM3 paleoclimatic model (Braconnot et al., 2007). The impact of human activities (i.e. anthropogenic

effects) was measured with the Human Influence Index (HII; Sanderson et al., 2002), which includes information about human population density, land use, infrastructure and human access.

2.2. Calculating phylogenetic and trait diversity

Phylogenetic and trait diversity are not entirely independent from either species richness or each other (Tucker, Davies, Cadotte, & Pearse, 2018). Also, traits usually have some degree of phylogenetic signal, so closely related species will tend to exhibit similar trait values (de Bello et al., 2017; Díaz et al., 2013; but see de Bello et al., 2015). To disentangle the effect of these three components of diversity, we calculated the phylogenetic diversity that is independent of species richness, and also the trait diversity that is independent of both species richness and phylogenetic diversity, using a rationale similar to de Bello et al. (2017) and Nascimento, Correia, Ruiz-Esparza, & Gouveia (2018). To do this, we developed an analytical approach based on distance matrices, following Diniz-Filho, Cianciaruso, Rangel, & Bini (2011) (see Fig. S1 in supporting information). For each assemblage (i.e. each grid cell), we calculated phylogenetic diversity (PD) using Faith's (1992) index, corresponding to the total branch length of a phylogenetic tree that connects all species within an assemblage. Afterwards, we calculated net phylogenetic diversity (nPD; herein called phylogenetic diversity for simplicity), i.e. the PD that is independent of species richness. To do this, we first created 1000 random assemblages from the species pool with the same species richness of each real assemblage, by shuffling species labels across the tips of the phylogeny. Second, we calculated nPD as the difference between the observed PD and the mean PD of the randomisations, divided by the standard deviation of the randomised PD values; therefore, nPD corresponds to the standardised effect size of each assemblage (Gotelli & Rohde, 2002). Negative nPD values correspond to assemblages with species that are phylogenetically clustered (i.e.

evolutionarily closer than expected by chance), whereas positive values indicate phylogenetically overdispersed assemblages (i.e. more distant than expected by chance).

Trait (functional) diversity was calculated using Petchey & Gaston's (2002) FD (herein named FD). This metric is conceptually similar to PD, and thus involves producing a distance matrix from a trait matrix (using a modified version of Gower's distance; Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009), converting it into a dendrogram (using UPGMA), and calculating the sum of branch lengths across it. In this case, the dendrogram was built using trait information of all mammal species present in the species pool. We also calculated net trait diversity (nFD), i.e. the FD that is independent of species richness, in the same way as nPD. Finally, we calculated phylogenetically-independent trait diversity from the residuals of the regression between the trait and phylogenetic distance matrices (using absolute distance values). These residuals were then used to construct a new dendrogram, which in turn was used to calculate the net phylogenetically-independent trait diversity (npiFD; herein trait diversity), following the same steps as for nPD and nFD. As in the case of nPD, negative values of npiFD indicate assemblages with species that are functionally clustered (i.e. species with trait values more similar than expected by chance), whereas positive values indicate trait overdispersed assemblages (i.e. more different than expected by chance).

2.3. Statistical analyses

Data on species richness, net phylogenetic diversity (nPD) and net phylogenetically-independent trait diversity (npiFD) per grid cell were divided into two subsets that differentiate between areas that were most affected by glacial conditions in the past from those that were less affected. These two subsets, herein named Northern and Southern Europe, were defined as the grid cells located

respectively north or south of the 0° C isotherm at the LGM (see Fig. 1), following Araújo et al. (2008) and Hortal et al. (2011) (see also Hewitt, 1999; Whittaker et al., 2007). All analyses were conducted separately for each one of these subsets. Differences in species richness, nPD and npiFD between northern and southern assemblages were assessed through a t-test for the comparison of two independent groups (parametric assumptions were tested visually; not shown), using Dutilleul's method (Dutilleul, 1993) that allows correcting the number of degrees of freedom to account for the pseudoreplication derived from the degree of autocorrelation in the variables. Further, we made a preliminary assessment on whether the relationship between each predictor variable and species richness, nPD or npiFD was either linear or quadratic through ordinary least squares (OLS) regressions (see Table S1), in order to decide the type of relationship that should be included latter on in subsequent analysis (see below). The relationship between HII and the different diversity variables was tested using a Pearson correlation and applying Dutilleul's correction (Dutilleul, 1993). All predictors were standardised to mean = 0 and standard deviation = 1.

Finally, we applied multigroup structural equation modelling (SEM; Grace, 2006; Shipley, 2000) to analyse the differences in the causal structure between current climate, climate stability, human influence and each response variable (i.e. species richness, nPD and npiFD). SEMs are particularly appropriate for testing whether multiple hypotheses hold up, as they allow evaluating a priori hypotheses describing the latent structure of the relationships among variables (Grace, 2006). In this type of analysis, a model with the same causal structure (i.e. same number and direction of relationships between variables) is fitted from all subsets simultaneously (in this work, the northern and southern biotas), but parameter values are allowed to vary freely between these subsets. We combined temperature and precipitation variables using composite variables (Grace

2006) to evaluate the aggregated effect of current climate and climate stability. Composite variables in SEMs are built by bringing together the paths of the component variables to the composite, and then creating a path between the composite and the response variable. This newly created path summarises the joint effect of the component variables on the response variable, and provides a way to measure the importance of conceptual variables that cannot be directly measured (in this case, climate as a whole).

To take into account spatial autocorrelation we included in the SEM model a set of spatial eigenvectors obtained through spatial eigenvector mapping (Diniz-Filho et al., 2008; Legendre & Legendre, 2012). To avoid high type I error rates related to eigenvector estimation, we first selected the eigenvectors that minimised the autocorrelation in model residuals, based on Moran's I (MIR *sensu* Bauman, Drouet, Dray, & Vleminckx, 2018). Including all these eigenvectors in the structural model would result in overparametrizing the model, inflating its degrees of freedom. This is one of the main problems to avoid when constructing SEM models (see Grace 2006). Thus, we solved the trade-off between minimising spatial autocorrelation and avoiding overparametrization by including in the SEM model only those eigenvectors that were significantly correlated (at $p < 0.05$) with the response variables. This assures that all spatially-structured variation in the dependent variables that is not accounted for by the predictors is included in the model while calculating its parameters. All parameters of the SEM model were estimated in presence of these eigenvectors, thereby avoiding potential problems due to spatial autocorrelation. Because the eigenvectors were used exclusively to account for spatial autocorrelation, their path coefficients are not shown. The final coefficients of determination (R^2 values) for all other paths in the model were calculated without the eigenvectors (following Diniz-Filho et al., 2008) because including them would have spuriously inflated the explained variability.

To fit the model, we first designed an *a priori* model in which we included the set of relationships that were theoretically important (see Fig. S2a). This initial *a priori* model did not fit the data well, so we re-specified the model by adding new relationships using modification indices as guidance. Modification indexes provide an estimate of the amount by which the chi-square would be reduced if a new relationship between two of the variables is added to the model. We sequentially added new relationships until an adequate model fit was achieved (Grace, 2006), taking into account only the relationships that have biological meaning. In this case, adding the correlations between the residuals of both species richness and trait diversity, and trait and phylogenetic diversity was sufficient to achieve a good model fit. After fitting the final model, we evaluated the stability of parameter estimation through a bootstrap. These procedures were repeated using alternative *a priori* models (Fig. S2b,c) that expressed different relationships between HII and species richness; models rendering higher Akaike's Information Criterion scores were ignored (i.e. the model depicted in Fig. S2b, where diversity affects HII, but not vice-versa). All SEM models were fitted using AMOS (Arbuckle, 2014). Complete SEM results can be found in the Appendix S2 in supporting information.

3. Results

The geographic distribution of species richness, phylogenetic diversity (nPD) and trait diversity (npiFD) does not coincide in Europe. Species richness increases from the northern and southern areas towards the centre of Europe, with the highest values being found close to the highest mountain chains (the Alps, Pyrenees, Carpathians and the Caucasus) and in the Balkan Peninsula (Fig. 1a). Southern biotas have more species than northern ones, in accordance with H1 (North: M = 47.141, SD = 14.235; South: M = 55.047, SD = 15.021; t-test with Dutilleul's correction: t (12)

342 = -10.304, $p < 0.001$). nPD values are higher in southern than in northern assemblages (North: M
343 = -1.743, SD = 0.745; South: M = -1.252, SD = 0.856; t-test with Dutilleul's correction: t (18) = -
344 11.585, $p < 0.001$), and significant phylogenetic clustering occurs in over 30% of northern
345 assemblages (i.e. grid cells), particularly in northern Russia (Fig. 1b; see Figure S3). Although
346 Southern European assemblages are dominated by a random phylogenetic structure, 21% of the
347 cells present a significant clustered pattern. However, despite nPD values being positive in the
348 south of the Caucasus mountains, no single cell is significantly overdispersed in any region (i.e.,
349 nPD is never higher than 1.96; Fig. 1b; see Figure S3). Phylogenetic diversity results therefore do
350 not totally support hypotheses H2.1 and H2.2. The geographic pattern of trait diversity is similar
351 to that of phylogenetic diversity, as npiFD values in the south are significantly higher than in the
352 north (North: M = -2.673, SD = 0.99; South: M = -1.551, SD = 0.792; t-test with Dutilleul's
353 correction: t (9) = -24.385, $p < 0.001$). However, in the case of trait structure, 75% of the northern
354 assemblages are significantly clustered (particularly north of current 0°C isotherm; Figs. 1c; see
355 Figure S3), while close to 70% of the southern assemblages present a random pattern. Note that
356 npiFD values tend to increase in southern assemblages (particularly in the Iberian and Italian
357 Peninsulas, and also south of the Caucasus), but are not significant. Therefore, results regarding
358 trait diversity agree with both H3.1 and H3.2. Human influence affects most facets of biodiversity,
359 particularly in northern assemblages (Fig. 2; Table S1). However, although species richness is
360 higher in areas with higher human influence (Fig. 2a; Pearson's adj. $r^2 = 0.345$; F (15) = 7.984;
361 $0.05 > p > 0.01$) as initially hypothesised (H4.1), there is no relationship between phylogenetic
362 diversity and human influence (Fig. 2b; Pearson's adj. $r^2 = 0.041$; F (21) = 0.9; $p = 0.354$). Also,
363 trait clustering is higher in areas with lower human influence (Fig. 2c; Pearson's adj. $r^2 = 0.389$; F
364 (9) = 5.866; $0.05 > p > 0.01$), contradicting H4.2 and H4.3.

According to SEM results based on the model depicted in Fig. 3, the importance of the direct and indirect effects of each explanatory factor also varies between northern and southern Europe (Fig. 3; Fig. S4). Current climate is consistently the main driver of diversity in both northern and southern regions (Fig. 3; Fig. S4), except for species richness in northern biotas, which is mainly driven by climate stability. Importantly, the sign of the direct effects of current climate is not constant between northern and southern biotas for both species richness and phylogenetic diversity (Fig. 3; Fig. S4). Current climate has an indirect effect on all facets of diversity through human influence in both northern and southern Europe, particularly over trait diversity in the south. In contrast, climate stability affects nearly all facets of diversity (the only exception is phylogenetic diversity in northern Europe), with no significant indirect effects occurring in any case through human influence (Fig. 3; Fig. S4). The alternative model depicted in Fig. S2c, where both HII and diversity are influenced by an unknown, common factor, presents the same model fit as that of the model described above, which indicates that both models are equivalent (for both models, $\chi^2 = 66.32$, AIC = 346.6).

4. Discussion

The diversity and structure of mammal biotas are not homogeneous across Europe and diverge in areas that were differently affected by past and present climatic events and anthropogenic changes. Northern European mammal assemblages have lower species richness, presenting phylogenetic and, more significantly, trait clustering, particularly north of the current 0° isotherm. Southern European assemblages, on the other hand, are richer, but have no particular pattern in neither phylogenetic nor trait structure. Current climate is the main driver of diversity (and of human influence), but climate stability also has an important effect on the species richness of northern

388 assemblages. Finally, human presence exerts direct and indirect effects on diversity, apparently
389 favoring species richness across Europe, but without leading to neither phylogenetic nor trait
390 clustering.

391 Despite the strong influence of past climate and human pressure, current climate is the most
392 important driver of large-scale gradients of European mammal diversity at the scale of our
393 analyses. Water and energy variables are known to impose constraints on species richness,
394 particularly at higher latitudes (Hawkins et al., 2003). However, the importance of different
395 climatic components may vary geographically (Gouveia et al., 2013; Hortal et al., 2011; Whittaker
396 et al., 2007). We found that such heterogeneity in the strength of the relationship between species
397 richness and current environment holds up for other aspects of diversity (see also Safi et al., 2011).
398 Indeed, current climate is highly correlated with species richness, particularly in the richer southern
399 areas, while its influence on phylogenetic and trait diversity is stronger in the species-poor
400 Northern Europe. Also, a high proportion of the variation in diversity that is accounted for by
401 current climate cannot be decoupled from human influence. Indeed, climate and primary
402 productivity can also drive the settlement of humans, which in turn impacts diversity distribution
403 (Luck, 2007). We provide additional support for the existence of these effects, as climate strongly
404 moderates human influence.

405 The general effects of current climate on the distribution of European mammals are
406 intertwined with the distinct imprint left by climate stability since the LGM. The strength of the
407 relationship between species richness and climate stability differs between northern and southern
408 biotas, becoming the most important driver of species richness in Northern Europe. These less
409 climatically stable northern areas, which were strongly affected by adverse conditions, also
410 suffered comparatively more extinctions associated with successive climate oscillations (Dynesius

411 & Jansson, 2000), which subsequently affected species distributions and led to lower species
412 richness in this region (in accordance with H1; Calatayud et al., 2016; Fløjgaard et al., 2011; Hortal
413 et al., 2011; Ordonez & Svenning, 2015; Svenning et al., 2015; Svenning & Skov, 2004). These
414 non-random extinctions lead to the disappearance of specific lineages and species with particular
415 traits, thereby selecting for generalist species and lineages. Our results support the existence of
416 such selection process, as there is a clear trend for northern European assemblages to include a
417 clustered selection of species from certain lineages and, most significantly, with specific traits (as
418 predicted by H2.1 and H3.1). Indeed, the vertebrate species that survived in this region show a
419 strong bias towards the extremes of the body size distribution (i.e., either small or large species;
420 Bhagwat & Willis, 2008), and Pleistocene climatic changes have been related to the selection of
421 large-bodied Carnivora species in northern Europe (Diniz-Filho et al., 2009). Subsequent
422 colonisation after temperatures rose and ice retreated was also dependent on the existence of
423 specific traits, including high mobility and short generation times –which are more frequent on
424 some lineages (Bhagwat & Willis, 2008; Jansson, Rodríguez-Castañeda, & Harding, 2013;
425 Ordonez & Svenning, 2016). Interestingly, the current location of the 0°C isotherm (which
426 associates with long periods of freezing temperatures throughout the year) marks a steep increase
427 in phylogenetic and, especially, trait clustering. This pattern may indicate that the constrain
428 imposed by such limit on the distribution of mammal species inhabiting the North of Europe is
429 timeless.

430 Differential survival and postglacial recolonisation would jointly explain the tendency for
431 more phylogenetically and, especially, trait clustered assemblages in northern biotas. However,
432 such trend is not a gradual decline of diversity with decreasing stability towards the north, rather
433 corresponding to distinct relationships between climate stability and both nPD and npiFD in

northern and southern Europe (see also Hortal et al., 2011). This pattern may result from the limited recolonisation of formerly glaciated areas by many species, due to limited dispersal ability and the migratory barriers posed by the Pyrenees, the Alps, the Balkans, the arid areas of inner Iberian Peninsula and the Mediterranean Sea (Ordonez & Svenning, 2015, 2016; see also Hewitt, 1999). Such limited recolonisation resulted in a depauperated Northern Europe, where species interactions or other community-level processes have had little influence on the post-glacial establishment of mammal assemblages. Therefore, differences in climate stability left no significant signal on the community structure within that region, or at least are hidden within the strong effects of current climate. Southern assemblages, in contrast, do not show a generalized pattern of clustered phylogenetic or trait diversity. The majority of them were not different from a random draw of species from the regional pool (although around a fifth of the cells in this region were phylogenetically clustered), thereby providing some support to hypotheses H2.2 and H3.2. Pleistocene climate changes were milder in these areas along the successive glacial-interglacial cycles (Ehlers & Gibbart, 2004), and so extinctions associated with repeated environmental filtering processes were probably less preeminent than in the north. Rather, these climatic oscillations may have promoted speciation processes in the south due to repeated cycles of vicariance and recolonisation (as in Rangel et al., 2018; see Schmitt, 2007), allowing the accumulation of diverging lineages and trait configurations (Jansson & Dynesius, 2002). Such combination of climatic refuge and increased diversification resulted in the higher phylogenetic and trait diversity of Southern European mammals, but not in the ecological saturation of landscapes that would have led to significantly overdispersed assemblages due to limiting similarity processes.

456 The relationship between human influence and mammal richness is, in general, positive,
457 as initially hypothesized. Results from SEM indicate that current climate also exerts indirect
458 effects on biodiversity through its effects on human influence, suggesting that both humans and
459 other mammal species thrive in areas that currently show higher productivity and/or certain
460 climates (Balmford et al., 2001; Fjeldså & Burgess, 2008). Indeed, the spread of human
461 populations has tracked the milder climate conditions (Timmermann & Friedrich, 2016), a pattern
462 also visible in their current distribution, particularly in the north of Europe. In this region, the
463 combination of overall low productivity and the preeminence of generalist species with large
464 distribution ranges (Davies, Purvis, & Gittleman, 2009; Hortal et al., 2011) may be promoting the
465 spatial coincidence in the establishment of human populations and (relatively) diverse mammal
466 faunas. However, contrary to our expectations, the areas of high human impact do not tend to hold
467 neither phylogenetic nor functionally less diverse assemblages. Long-term human occupation
468 throughout the Pleistocene and Holocene may have increased local habitat diversity and landscape
469 heterogeneity, thus promoting higher species richness and the establishment of species with very
470 different adaptations and ecological roles (van Rensburg, Chown, & Gaston, 2002; see also Stein,
471 Gerstner, & Kreft, 2014).

472 Note, however, that these patterns correspond to the observed distribution of extant species,
473 after the extinction of those species more intolerant to humans. This effect increases the proportion
474 of species in the regional pool that can thrive in highly-impacted areas, and so these areas host
475 comparatively richer assemblages (Araújo, 2003), that still represent the overall trait and
476 phylogenetic structure of the species pool. In contrast, the imprint of human influence on
477 biodiversity does not show a direct relationship with climatic stability. This is perhaps due to the
478 highly idiosyncratic nature of mammal extinctions in Europe during the Pleistocene (see Crees et

al., 2016; Lorenzen et al., 2011; Santini, González-Suárez, Rondinini, & Di Marco, 2017). Some species tracked climate changes, becoming extinct by humans only in periods when the extent of their suitable areas was substantially reduced (e.g. woolly mammoth; Nogués-Bravo et al., 2008). In contrast, other species were seemingly not affected by climatic oscillations nor human colonisation (e.g. reindeer; Lorenzen et al., 2011). These species may have coped with the spread of human populations partly because they did not suffer strong reductions in the extent of their climatically suitable areas. They might also possess traits that allowed their persistence in landscapes increasingly impacted by humans (e.g. horse; Lorenzen et al., 2011), like being evasive or inconspicuous, having short generation times or being able to feed on resources that persist or increase in human-transformed habitats. These traits would have contributed to the different selection of species and lineages between northern and southern Europe discussed above, but without generating a clear (i.e. smooth) geographic gradient of progressive influence of humans in more stable areas.

It is also important to mention that other factors that were not specifically considered in this study might be affecting both human influence and biodiversity, thereby causing the correlation between them, as indicated by the similar power of the alternative SEM model (Figure S2c). This model implies the existence of an extrinsic factor affecting simultaneously both predictors and dependent variables in the structural equation model. Although it is hard to think of a missing factor operating directly with similar intensity on the dynamics of climate, land use and diversity, this serves as a cautionary note that our results should be complemented with further research on the effects of other past and recent factors, such as long-term landscape dynamics or the effects of pathogens and parasites (see, e.g., Ricklefs, 2015).

To summarise, by accounting for the effects and interactions between current and past drivers of diversity, we showed that current European mammal diversity is affected by both contemporary and long-term global change effects, but in spatially complex and, sometimes, counterintuitive ways. The analytical approach used here allows accounting for variations in species diversity, lineages and traits within a common framework, separating their largely shared variations into independent variables (see de Bello et al., 2017; Nascimento et al., 2018 for similar approaches). This wider and more complete overview of the factors acting behind the current distribution of biodiversity allows a deeper understanding of the causes and consequences of global change impacts on biodiversity (see, e.g. Mouillot et al., 2013). Indeed, the spatial idiosyncrasy of the relationship between different aspects of biodiversity and climate, climate changes and human impacts calls for reconsidering the common assumption that strong disturbances and harsh conditions unavoidably lead to lower levels of phylogenetic and trait diversity.

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6. Data accessibility statement: All data used in this article comes from public sources and will be archived at DIGITAL.CSIC public repository (https://digital.csic.es/handle/10261/179077) upon acceptance of the manuscript. The final DOI of the data will eventually be included at the end of the article.

7. Figures

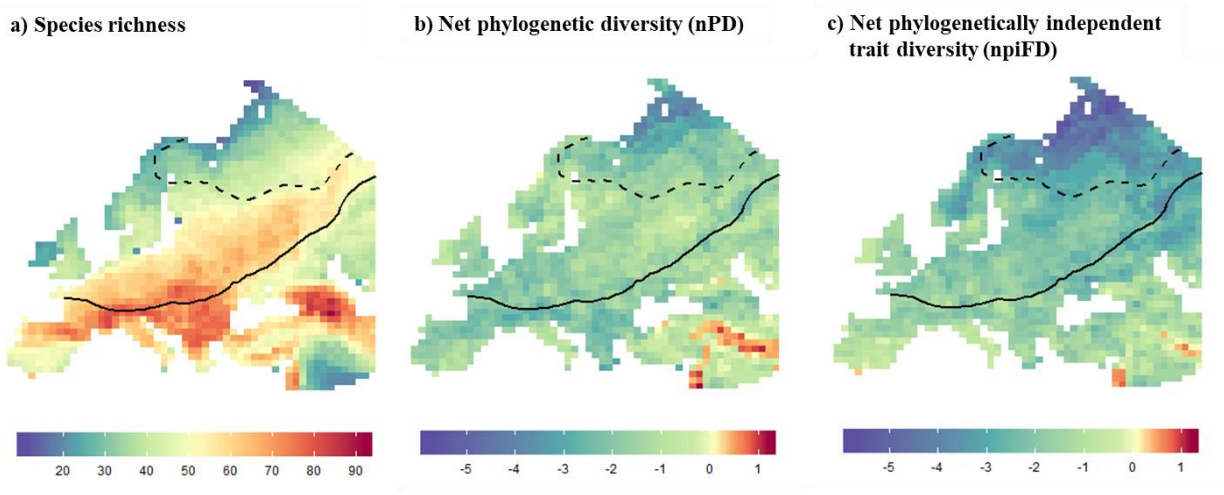


Figure 1. Geographic distribution of mammal (a) species richness, (b) net phylogenetic diversity and (c) net phylogenetically-independent trait diversity across Europe. The solid black line indicates the position of the 0°C isotherm at LGM (21 ka), while the dashed line indicates its current location. (b) and (c) are represented using the same scale, and values below -1.96 indicate assemblages with phylogenetic or trait clustering, respectively.

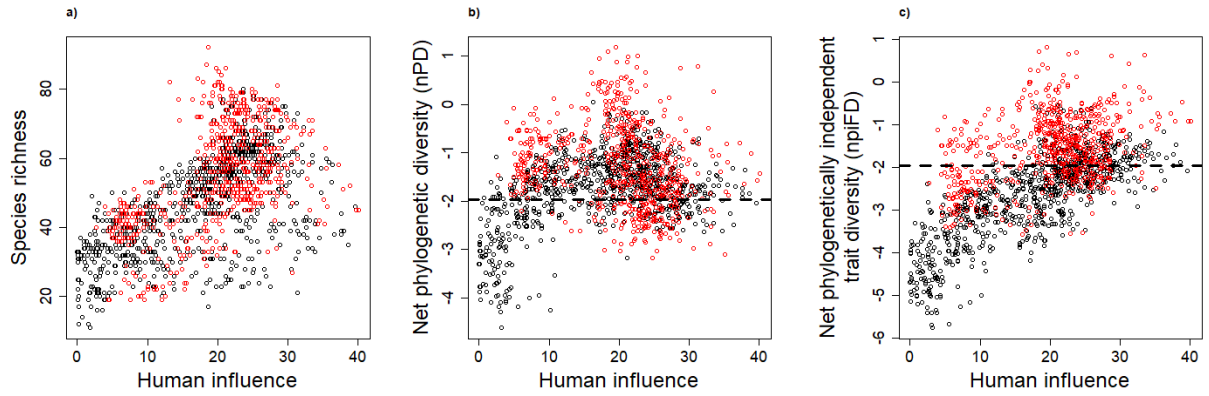


Figure 2. Relationship between human influence and (a) species richness, (b) net phylogenetic diversity (measured as nPD) and (c) net phylogenetically-independent trait diversity (measured as npiFD) in Europe (see supporting information, Table S1). Red dots represent grid cells located south of the 0° C isotherm of the Last Glacial Maximum, and black dots represent those located north of that line. The dashed line indicates SES = -1.96, meaning that values falling below it are statistically significant (i.e. p-value<0.05).

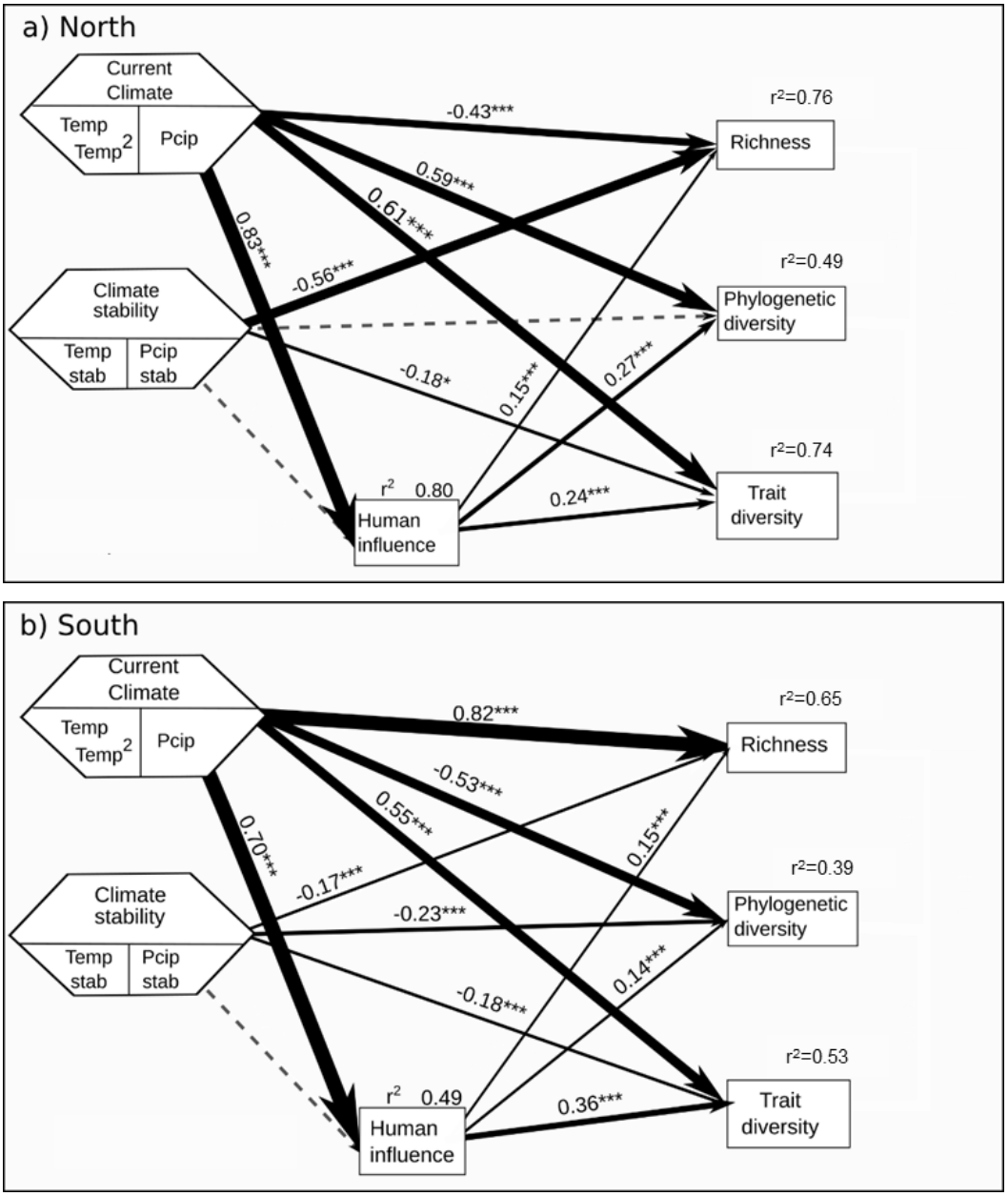


Figure 3. Structural Equation models (SEMs) for the mammal diversity of (a) Northern Europe and (b) Southern Europe. Species richness was measured as number of species, phylogenetic diversity as net phylogenetic diversity (nPD) and trait diversity as net phylogenetically-independent trait diversity (npiFD) (see main text for details). Model fit parameters: $\chi^2 = 66.32$; $p = 0.53$; d.f. = 64. Numbers indicate the standardised path coefficients; arrow thickness is proportional to coefficient value; and dashed lines correspond to non-significant relationships. Coefficients of determination of endogenous variables that act as response variables are also represented. The correlations between the errors of exogenous variables are not shown.

Supporting Information– Appendix S1. Long-term climate changes, current climate and human impacts determine the geographic distribution of European mammal diversity

Table S1. Results of the exploratory linear ordinary least squares (OLS) regressions assessing the relationship between species richness, phylogenetic diversity (nPD) and trait diversity (npiFD) of mammal assemblages, and several descriptors of current climate, climate stability and anthropogenic effects. Quadratic terms were evaluated for all predictors, but only significant relationships are shown.

			Species richness		Phylogenetic Diversity		Trait Diversity	
	Set of variables	Variable	Coefficient	Adj. R^2	Coefficient	Adj. R^2	Coefficient	Adj. R^2
Northern Europe	Current Climate	Current Temperature	**1.744**	-	**0.094**	-	**0.167**	-
		Current Temperature^2	**-0.092**	**0.349*** **	**-0.011**	**0.466*** **	**-0.002**	**0.704*** **
		Current Precipitation	**-0.03**	**0.14*** **	**0.001**	**0.041*** **	**0.001**	**0.033*** **
	Climate stability	Temperature Stability	**-1.137**	**0.457*** **	-0.002	-0.001	**-0.011**	**0.008** **
		Precipitation Stability	**-0.046**	**0.316*** **	$3.116x10^{-5}$	-0.001	**-0.002**	**0.116*** **
	Anthropogenic effects	Human Influence	**0.958**	**0.375*** **	**0.036**	**0.194*** **	**0.085**	**0.612*** **
Southern Europe	Current Climate	Current Temperature	**3.711**	-	**0.018**	-	**0.306**	-
		Current Temperature^2	**-0.171**	**0.331*** **	**0.002**	**0.149*** **	**-0.007**	**0.415*** **
		Current Precipitation	**0.05**	**0.599*** **	**-0.002**	**0.324*** **	**-0.001**	**0.022*** **
	Climate stability	Temperature Stability	**2.076**	**0.061*** **	**-0.204**	**0.184*** **	**-0.071**	**0.025*** **
		Precipitation Stability	**0.055**	**0.122*** **	**-0.001**	**0.0193*** **	**$-4.938x10^{-4}$**	**0.002*** **
	Anthropogenic effects	Human Influence	**1.063**	**0.274*** **	**-0.026**	**0.048*** **	**0.039**	**0.129*** **

*0.05 > P > 0.01; **0.01 > P > 0.001; ***P < 0.001.

Coefficient corresponds to the regression coefficients; Adj. R^2 is the adjusted R^2. Values in bold are statistically significant.

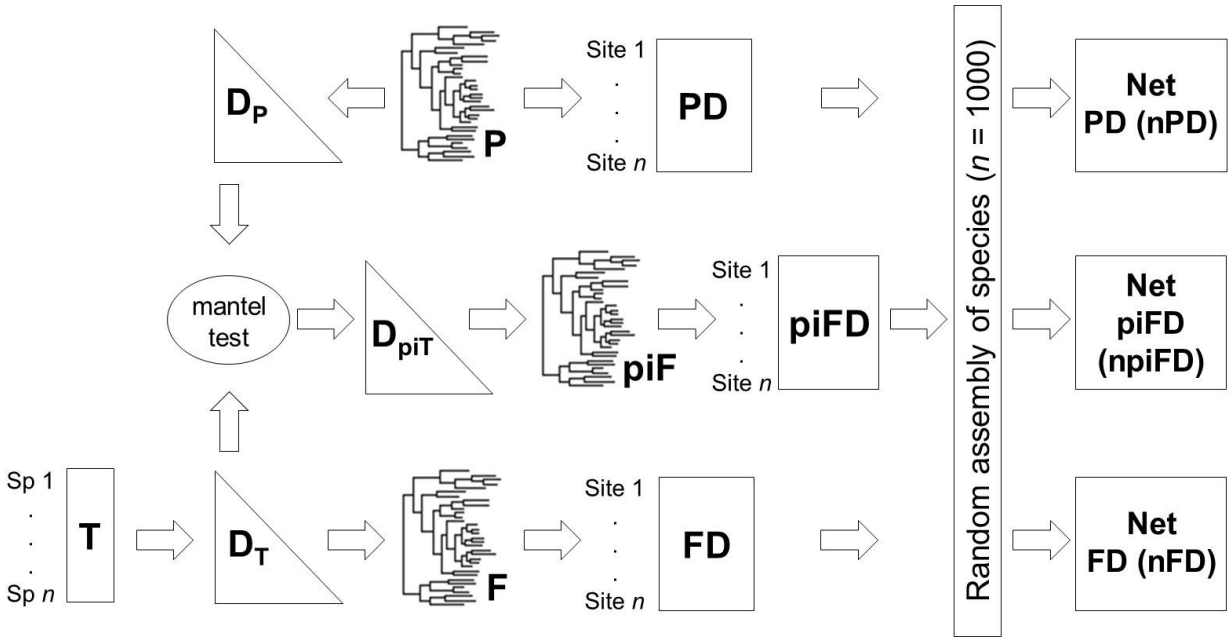


Figure S1. Scheme of the hierarchical protocol used to separate the net phylogenetic and trait diversity components independent from species richness, and the net phylogenetically-independent component of trait diversity. Triangular distance matrices (Dp and Dt) based on phylogenetic (P) or trait (T) data, respectively, were obtained from either known phylogenies or trait values. Net phylogenetic diversity (PD) and trait diversity (FD) were calculated according to the branch lengths of their corresponding trees, and their richness-independent variations (nPD and nFD) were calculated as the net departure from 1000 random assemblages of the same number of species, gathered from the species present in the regional pool. Phylogenetically independent trait diversity (piFD) and net phylogenetically-independent trait diversity (npiFD) were obtained from a matrix of phylogenetically-independent trait distances (DpiT), calculated as the partial component of trait distances in a matrix regression between trait and phylogenetic distance matrices.

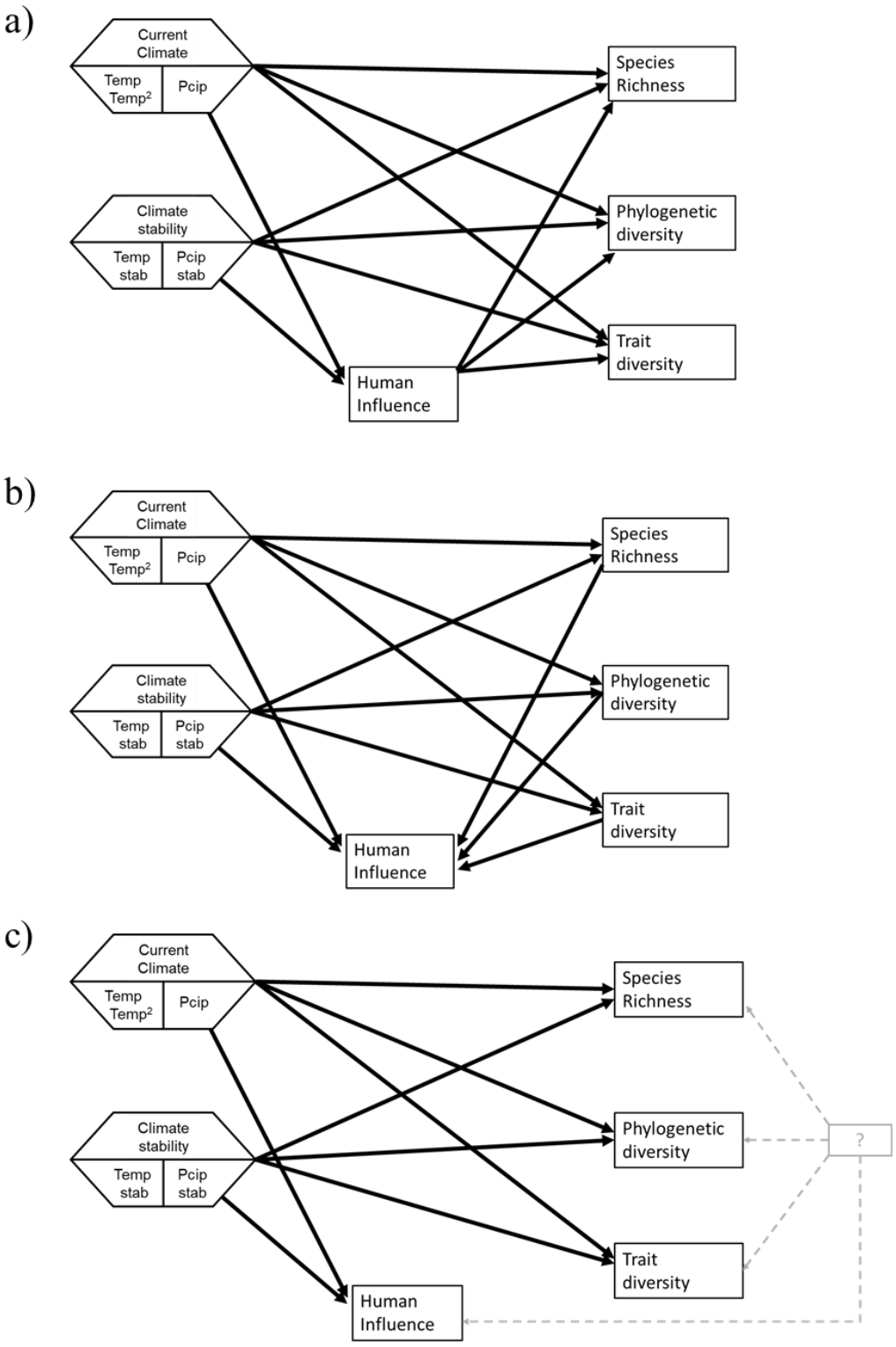
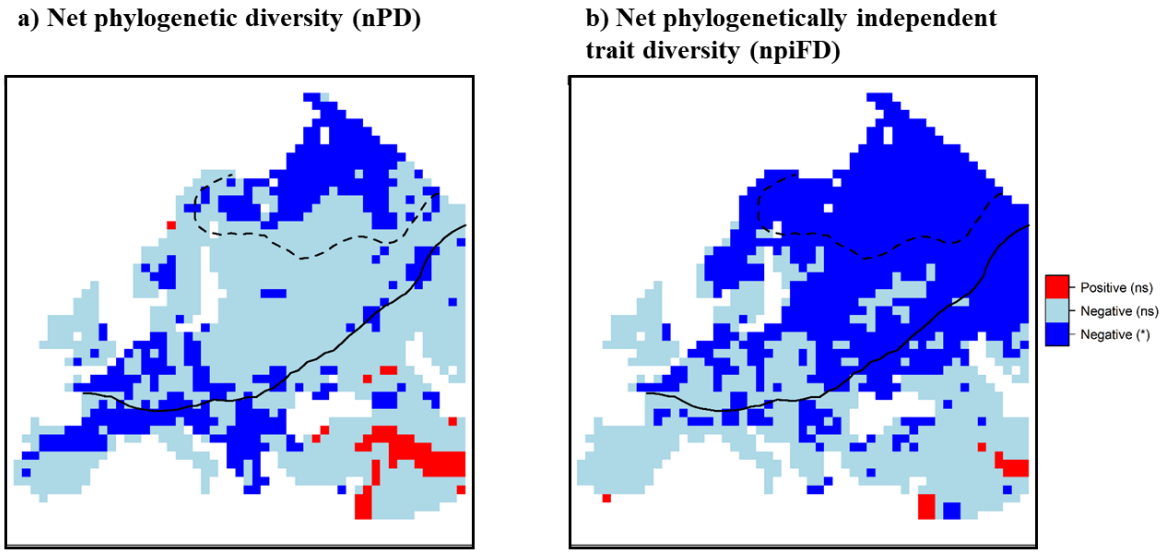


Figure S2. Scheme of the *a priori* models that summarise the initial hypothesis on how endogenous (response) and exogenous (explanatory) variables are related. Model a) was the one used in the study, while b) and c) correspond to altermative models.



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833 Figure S3. Geographical distribution of the statistical significance of mammal (a) net
834 phylogenetic diversity (nPD) and (b) net phylogenetically-independent trait diversity (npiFD)
835 across Europe. The solid black line indicates the position of the 0°C isotherm at the Last Glacial
836 Maximum (21 ka), while the dashed line indicates its current location. Red cells indicate non-
837 significant positive values of both nPD and npiFD (i.e., $0 < nPD/npiFD < 1.96$), while grey cells
838 indicate non-significant negative values (i.e., $-1.96 < nPD/npiFD < 0$) and blue cells indicate
839 significant negative values (i.e., $nPD/npiFD \leq -1.96$).

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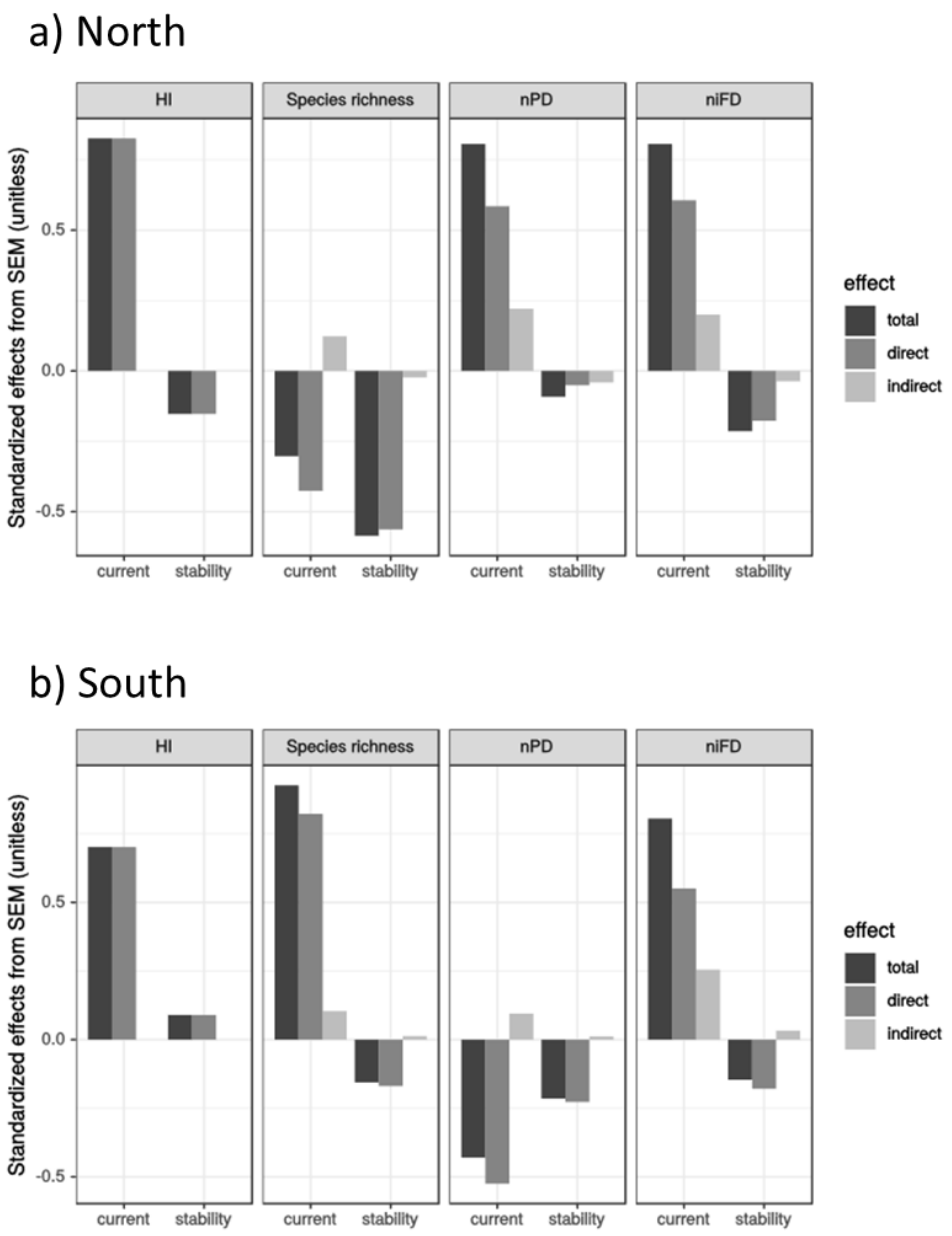

842

843 Figure S4. Total, direct and indirect standardised effects (through human influence) of both
844 current climate and past climate stability, obtained from the path coefficients of the structural
845 equation models (SEMs) for mammal diversity (species richness, phylogenetic – nPD, and trait
846 diversity – npiFD; see main text for more details) in (a) Northern Europe and (b) Southern
847 Europe.

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849

850 File GEB-2019-0174.R2.xls. Appendix S2. Complete results of the SEM analysis for northern
851 and southern Europe. The document includes two sheets. The first one “Fit summary” reports the
852 results of the model before including the composite variables, and is useful for checking the
853 effects of current climate (three variables: temperature, temperature² and precipitation) and
854 climate stability (two variables: stability in temperature and precipitation) individually. The
855 second sheet “composite summary” reports the results of the model once the composite variables
856 are included, and is useful to check the effects of current climate and climate stability as a whole.
857 Both sheets include four tables. Table a: Coefficients of the relationships or regression weights;
858 table b: covariance between the exogenous variables; table c: correlation between the exogenous
859 variables; table d: percentage of explained variability or squared multiple correlations. Also, each
860 table contains two parts, the left panel shows the analysis for northern Europe and the right panel
861 shows the results of southern Europe.